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Abstract: An F_1 mapping population was bred by crossing an accession of wild cardoon with a single Argentinian globe artichoke plant of the variety "Estrella del Sur FCA" with a view to generate new *C. cardunculus* linkage maps. Genotyping was conducting using a set of 553 SRAP, SSR, AFLP and SNP markers. The 1,465.5 cM map based on the segregation of alleles present in the wild cardoon parent comprised 214 loci distributed across 16 linkage groups (LGs), while the 910.1 cM globe artichoke based map featured 141 loci falling into 12 LGs and the total length. Three of the morphological traits (inflorescence spininess, leaf spininess and head color) for which the parents contrasted were inherited monogenically, and the genes conditioning them were mapped. A set of 48 co-dominant loci was used to align the LGs with those derived from a reference SSR-based consensus map of the species.

Keywords: *Cynara cardunculus*, globe artichoke, cardoon, molecular markers, linkage groups, genetic map.

Introduction

The *Asteraceae* species *Cynara cardunculus* L. (*2n=2x*=34) includes two domesticated taxa, namely the globe artichoke (var. *scolymus*) and the cultivated cardoon (var. *altilis*), as well as the wild cardoon (var. *silvestris*), commonly considered to be the wild ancestor of both domesticated forms (Rottenberg and Zohary 1996; Lanteri *et al*. 2004). The species is highly heterozygous and suffers from inbreeding depression when self-fertilization is enforced (Cravero *et al*. 2002). Since inter-taxon hybrids are viable and fertile, globe artichoke improvement programmes can readily access germplasm across the whole species complex (Portis *et al*. 2009). Despite the impact of inbreeding depression, conventional breeding has succeeded in producing a number of high quality and genetically uniform seed-propagated globe artichoke varieties (López Anido *et al*. 2010; Garcia *et al*. 2006).

Up to now, the mode of inheritance of only a few traits (earliness, color, spininess and tightness of the head) has been investigated in detail (Pécaut 1993; López Anido *et al*. 1998; Mauromicale and Ierna 2000; Cravero *et al*. 2005; Lanteri *et al*. 2006; Portis *et al*. 2012). The development of a genetic linkage map simplifies the genetic analysis of trait variation, particularly for those traits which are polygenically inherited. The definition of trait/marker linkages provides a tool for accelerated selection via marker assisted selection (Young 1999). The first such maps for globe artichoke was developed by Lanteri *et al*. (2006) and was based on 204 loci which fell into 18 linkage groups (LGs) for the female map and 180 loci distributed in 17 LGs for the male one. Since then, marker density of the original maps has been increased (Acquadro *et al*. 2006; 2009) and a number of other maps have been elaborated (Sonnante *et al*. 2011; Portis *et al*. 2012).

Building molecular marker based linkage maps has relied on a number of marker technologies. A particularly flexible and effective one, termed “sequence related amplified polymorphism” (SRAP), has been proposed by Li and Quiros (2001). SRAP advantages include simplicity, robustness, a reasonable throughput capacity and the ready sequencing of specific fragments included in the amplicon. The design of the primers ensures that the majority of polymorphisms arise due to variation in the length of intron, promoter and spacer regions (Lin *et al*. 2003). Approximately half of all of SRAP markers are located within the genic portion of the genome (Lin *et al*. 2003; Sun *et al*. 2007).

Here, we present genetic linkage maps of *C. cardunculus* based on a cross between an accession of wild cardoon and a single plant belonging to the open pollinated Argentinian globe artichoke variety “Estrella del Sur FCA”. Most of the genotypic data needed for linkage map construction were derived from SRAP analysis, although other PCR-based markers were also included to allow cross-referencing with the consensus

map recently produced by Portis *et al*. (2012). The resulting maps were used to identify and locate the major loci controlling three key agronomic traits.

Materials and methods

Plant materials and DNA extraction

A mapping population was generated by pollinating a local accession of wild cardoon with a single plant of "Estrella del Sur FCA" ("Est"). The putative F_1 seeds were sown in a greenhouse, and seedlings at the fourth true leaf stage were transplanted, together with both crossing parents, into a loamy soil field at the Experimental Field Station of the Universidad Nacional de Rosario (33º1'S; 60º53'W). This site experiences a temperate climate and an average annual rainfall of 950 mm, and is typical of the zone in Argentina where most of the country's globe artichoke is produced (Cravero *et al.* 2010). The inter-row spacing was 1.4 m and the spacing between plants within each row was 80 cm. Genomic DNA of the presumptive hybrids and the parental genotypes was extracted from fresh leaf using a DNeasy Plant mini Kit (Qiagen). The hybrid status of each population member was verified with two SSR (simple sequence repeats) markers CELMS-30 and -37 (Acquadro *et al*. 2009) that were polymorphic between parents. This resulted in the identification of a set of 91 true F_1 hybrids.

Genotypic analysis

The mapping population was genotyped using SRAP, SSR, AFLP (amplified fragment length polymorphism) and SNP (single nucleotide polymorphisms) markers. The number of SRAP primer combinations (PCs, Table 1) was 25. We used the protocol described by Cravero *et al*. (2007), except that each reaction only contained 1U Taq polymerase. The resulting amplicons were separated by electrophoresis through 6% (w/v) denaturing polyacrylamide gels, and then visualized by silver staining (Bassam *et al*. 1991). The AFLP procedure followed that of Vos *et al.* (1995), as modified by Lanteri *et al*. (2004). Briefly, the genomic DNA was digested with *Eco*RI and *Taq*I and ligated to a standard adaptor oligomer. The product of the ligation reaction represented the template for a PCR driven by a pair of primers complementary to the adaptor sequences plus one selective nucleotide at their 3' end (*Eco*RI+A and *Taq*I+T). A second PCR followed driven by one of 16 PCs (Table 2). The resulting amplicons were separated by electrophoresis through a 6.5% denaturing polyacrylamide gel, and

detected using a Gene ReadIR 4200 system (LI-COR) (Jackson and Matthews 2000). The set of SSRs comprised 247 loci and were assayed using a combination of CELMS (*Cynara* Enriched Library MicroSatellite; Acquadro *et al*. 2009) and CyEM (*Cynara* Expressed Microsatellite; Scaglione *et al*. 2009) markers. An initial screen was performed using as template DNA from the two parentals and six of the F_1 progeny, in order to identify those markers which were more informative. Only the selected markers were applied to the full mapping population. The PCR conditions applied followed the recommendations of the markers developer and the amplicons were separated in the same way as the AFLPs. SNP markers were directed at seven genes involved in the synthesis of caffeoylquinic acids, namely *HCT, HQT, C3'H, C4H, 4CL, Acyltransf_1 and _2* (Comino *et al*. 2007; 2009; Moglia *et al*. 2009; Menin *et al*. 2010). The assay was based on a tetra-primer ARMS-PCR (amplification refractory mutation system) protocol (Ye *et al*. 2001), with the amplicons being separated by electrophoresis through 2% w/v agarose gels and visualized by ethidium bromide staining.

Fragments generated by the SRAP and AFLP assays were treated as dominant markers, with each marker named according to the PC used to generate it (Tables 1 and 2) and the estimated size of the fragment; for example, locus 1.800.190 is an AFLP fragment of 190-bp length amplified by PC *Eco*+ACC/*Taq*+TTT. SSR and SNP loci were scored as co-dominant markers and identified by the primer pair used in the assay.

Phenotypic analysis

The parents differ from one another in spininess of the leaf and head bracts, and by their head color: "Est" is non-spiny and forms purple heads, while the wild cardoon accession is spiny and forms green heads. The presence/absence of spines on fully developed leaves and bracts, and head color was scored over two consecutive seasons (2008 and 2009). Goodness of fit between the observed and expected segregation according to a proposed inheritance model was evaluated using the χ^2 test.

Construction of the linkage maps

The marker loci were either (1) maternal testcross markers which segregated only in the female (wild cardoon) gamete, giving a ratio of 1:1 in the F_1 population; (2) paternal testcross markers which segregated only in the male (globe artichoke) gamete, giving a ratio of 1:1 in the F_1 population; and intercross markers, which segregated in both gametes, producing a segregation ratio of either 3:1 (for the SRAP and AFLP markers) or 1:2:1 (SSR and SNP markers) in the F_1 population. The two-way pseudo-testcross mapping strategy described by Weeden (1994) and Grattapaglia and Sederoff (1994) was used to develop two independent linkage maps,

one for each parental genotype. Goodness-of-fit between the observed and expected segregation ratios was determined by a χ^2 test. Only markers either fully consistent with monogenic segregation ($\chi^2 \leq \chi^2_{\alpha=0.1}$) or showing only minor distortion ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.01}$) were used for the construction of the maps. Those for which the segregation was highly distorted ($\chi^2 > \chi^2_{\alpha=0.01}$) were included in a second round of mapping only when their presence induced no alteration in local marker order. The LOD threshold for accepting an LG was 5.0, as estimated by JoinMap4.0 software (Van Ooijen 2006). The JoinMap settings applied were Rec=0.40, LOD=1.0 and Jump=5. Recombination values were converted to genetic distances using the Kosambi (1944) mapping function. Intercross markers were used to identify homologous LGs. The LGs derived from the wild cardoon parent have been labeled "Wild" and those from the globe artichoke parent as "Est" (Fig. 1A-C, Table 3). Linkage maps were drawn using MapChart 2.2 software (Voorrips 2002)

Alignment of the "Wild" and "Est" LGs with the SSR-based consensus LGs

The SSR and SNP markers were used to align the *de novo* LGs with those derived by Sonnante *et al.* (2011) and Portis *et al*. (2012). To achieve this, a consensus map, based exclusively on SSR and SNP markers, was assembled from the SSR and SNP segregation data collected from the "Romanesco C3" (globe artichoke) x "Altilis 41" (cultivated cardoon) mapping population described by Portis *et al*. (2012). This SSR-based consensus map had an overall length of 1068.0 cM, comprising 217 SSR and ten SNP loci arranged into 20 LGs (LOD threshold >6.0). The haploid chromosome complement was recovered by lowering the LOD threshold to 5.0. These 17 SSR-based consensus LGs are hereafter referred to as "SSR-Ref_LGs", applying the same I through XVII numbering system employed by Portis *et al*. (2012). When bridge markers linked the "SSR-Ref_LGs" with the "Wild" and "Est" ones, the latter have been numbered accordingly (Fig. 1 A-C, Tab. 3).

Results

Markers segregation

The SRAP analysis generated 336 informative fragments, representing a mean of 13.4 (range: 4-51) per PC. Of these, 186 segregated as expected in the maternal gametes, 130 as expected in the paternal gametes, while 20 were inferred to have been in the heterozygous state in both parental lines (intercross markers). The mean number of informative AFLP markers per PC was 8.4 (range: 1-27), so that in all, 135 loci segregated, of which

78 segregated only in the female gamete, 47 in the male gamete and the remaining ten were intercross markers. On the whole, of the combined 441 SRAP and AFLP testcross markers, 59.9% segregated in the wild cardoon parental genotype, while 40.1% in "Est". The segregation of ~24% (112 loci) of the SRAP and AFLP markers was distorted ($\chi^2 > \chi^2_{\alpha=0.1}$).

Of the 61 CELMS SSRs tested, 28 were informative between the parents; of these 14 segregated only among the female gametes, 13 among the male, and only one was an intercross marker. Similarly, of the 186 CyEM SSRs tested, 25 segregated only among the female gametes, 17 among the male, and seven were intercross markers. Two of the SSR loci suffered a minor degree of segregation distortion ($\chi^2_{\alpha=0.05} < \chi^2 \leq \chi^2_{\alpha=0.01}$). Five, out of the seven SNP loci genotyped, segregated in the mapping population. The *HCT* marker segregated only among the female gametes, whereas those for *HQT*, *C3'H*, *4CL* and *Acyltranf_1* segregated only among the male gametes.

Phenotyping

The three morphological traits investigated segregated consistently with a 1:1 ratio, suggesting that, in the analyzed progeny, all these traits are controlled by single genes with alternative alleles in each of the parents. The χ^2 values associated with these ratios were, respectively, 5.13 for the presence/absence spines on the heads, 2.78 for the presence/absence spines on the leaf, and 1.53 for purple-green *vs* purple heads ($\chi^2 \leq \chi^2_{\alpha=0.01}=6.63$).

Linkage maps construction and their alignment

Five hundred fifty-six markers were used for maps construction (553 molecular and 3 phenotypic markers). The genetic map constructed from the female gametes (the "Wild" map) was based on segregation at 344 loci, while that from the male gametes (the "Est" map) was based on 250 loci. The number of intercross markers was 38. The linkage analysis resulted in the placement of 345 loci across both maps, comprising 187 SRAP markers, 89 AFLP markers, 64 SSR loci, three SNP loci and three phenotypic traits.

The "Wild" map featured 214 loci distributed over 16 LGs, each defined by between five and 34 loci (mean 13.4), their length ranging from 30.1 to 153.1 cM (mean 91.6cM). The overall map length was 1,465.5 cM and the mean inter-marker distance was 7.4 cM (range 3.1–15.0 cM). The placement of one SNP and 28 SSR loci allowed the alignment of the 16 LGs with 13 consensus SSR-based map LGs (Table 3; Fig. 1A-C); three pairs of "Wild" LGs (Ia and Ib, Va and Vb, XVa and XVb) each corresponded with a single consensus

SSR-based one. Among the loci showing segregation distortion, 28 were successfully integrated within ten of the LGs. Clusters of distorted loci were detected on Wild_VIII (four loci) and Wild_XII (ten loci) (Fig. 1 B-C).

The "Est" map comprised 141 loci grouped into 12 LGs, which covered a genetic length of 910.1 cM. The individual LGs varied in length from 12.5 to 153.7 cM (mean 75.9 cM), containing between three and 23 (mean 11.8) loci. The mean inter-locus distance was 7.1 cM (range 3.7–19.3 cM). The placement of 19 SSR and two SNP loci allowed 11 of these LGs to be aligned with nine of the reference LGs (Table 3; Fig. 1A-C). Two pairs of "Est" LGs (VIIIa and VIIIb, Xa and Xb) each corresponded with a single consensus SSR-based one. The remaining LG was labeled "Est_n.a." (n.a.= not aligned) in Table 3 and Fig. 1C. Among the loci showing segregation distortion, 29 were successfully integrated within eight of the LGs. Two clusters of distorted loci were detected on Est_Xb (one comprising two and the other three loci), along with one cluster on Est_XII (ten loci) and a further one on Est_XVII (three loci) (Fig. 1B-C).

The genes underlying the presence/absence of head spines (Sp_{Head}), the presence/absence of leaf spines (Sp_{Leaf}) were represented on the "Est" map (LG VIIIa), and the one responsible for head color (*ColorHead*) was located on LG Wild_Va.

Ten of the 38 intercross markers (four SRAP, four AFLP and two SSR) were assignable to a specific LG in both maps (three each on IX and XII and four on XI), which aided the identification of homology between the "Wild" and "Est" LGs. Three other pairs (II, III and VIII) were identified as being homologous, based on their alignment with the reference SSR-based map (Tab. 3, Fig. 1 A-C). The distribution across 12 "Wild" and nine "Est" LGs of the 31 markers shared with the map generated by Sonnante et al. (2011) is also shown in Table 3.

Discussion

A population arising from the cross between wild cardoon and a globe artichoke variety was generated with the view to construct a linkage map and locating the genes underlying the presence/absence of spines on the heads and leaf, and pigmentation of the heads. The high level of inbreeding depression experienced by *C. cardunculus* (Cravero *et al*. 2002) prevents either backcross, F_2 or recombinant inbreed line populations being used for mapping quantitative traits, so instead the double pseudo-testcross approach was taken, as also successfully used by Lanteri *et al.* (2006), Portis *et al*. (2009) and Sonnante *et al*. (2011). Mapping population individuals obtained from other globe artichoke x wild cardoon crosses have been shown to vary widely with respect to both

quantitative and qualitative characters (Sonnate *et al*. 2011; Lanteri *et al*. 2012), confirming that a high level of heterozygosity has been retained in both wild and cultivated germplasm (Portis *et al*. 2005a, 2005b; Mauro *et al*. 2009, 2012).

The present linkage maps were based on a variety of molecular marker types. The choice of SRAP PCs reflected prior experience (Cravero *et al.* 2007) and, as SRAP genotyping generated most of the markers applied, these loci constituted the major backbone of the two maps. Since its development some ten years ago, SRAP genotyping has been deployed in a range of plant species for estimating levels of genetic diversity (Cravero *et al*. 2007; Esposito *et al*. 2007; Aneja *et al*. 2012), gene tagging (Martin *et al*. 2008; Zhang *et al.* 2011) and map construction (Lin *et al*. 2003; Sun *et al*. 2007; Xue *et al*. 2010). However, here we report its first usage for a genetic mapping in *C. cardunculus*.

A comparison of heterozygosity between the mapping parents used by Portis *et al*. (2009) showed that fewer loci were informative in the cultivated cardoon than in the globe artichoke variety "Romanesco C3". An explanation for this difference reflected the fact that while the latter is propagated vegetatively, the former is a seed-propagated variety. Clonal propagation allows the maintenance of high heterozygosity levels, but seed propagation can introduce an element of purifying selection to stabilize production. In contrast, the parental lines used by Sonnante *et al*. (2011) (one a globe artichoke, the other a wild cardoon) produced a pair of maps in which the cultivated parent map include more loci than the wild parent one. In the present case, the wild cardoon-based map was based on a higher number of loci than the globe artichoke one (214 vs 141 markers) and was around 50% longer (1,465.5 cM *vs* 910.1 cM), implying that the level of heterozygosity in the wild cardoon parent is higher than in the domesticated type. Indeed, the latter was selected from an open pollinated population on the basis of some key commercial traits (Garcia *et al*. 2006), and it was expected that this selection would have reduced its global level of heterozygosity.

Segregation distortion is commonplace in mapping populations, including an intra-taxon one in *C. cardunculus* where it affected ~10% of the loci (Lanteri *et al.* 2006). Here, the segregation of some 19% of mapped loci was distorted, and this higher level may simply reflect the greater genetic separation between the parents of the population (Grandillo and Tanksley 1996; Verde *et al.* 2005). Clusters of distorted markers were detected in both the "Wild" and the "Est" maps. Since the direction of segregation bias within each cluster was unidirectional, the suggestion is that the basis of the phenomenon is biological, rather than it being due to scoring error or chance (Fishman *et al*. 2001).

The mapping of the three morphological traits considered was consistent with each being determined by a single gene. The spininess of the head trait has been known for some time to be determined by the gene *Sp*, where the dominant allele determines lack of spininess (Pochard *et al.* 1969; Basnizki and Zohary 1994). The wild cardoon parent used here was therefore presumably of genotype *spsp*, while that of "Est" was *Spsp*. The homozygous state prevented its location in the "Wild" map, but it was successfully located to LG VIIIa on the "Est" map. The gene underlying the presence/absence of leaf spines (Sp_{Leaf}) appeared to be tightly linked to *Sp*. The presence of recombinants in the F_1 progeny indicates that this trait is therefore controlled by a locus distinct from *Sp*. The non spiny type is conditioned by the presence of at least one dominant allele (Sp_{Leaf}-), while the recessive homozygote $sp_{Leaf}sp_{Leaf}$ produces spiny leaves. At the genetic level therefore, we propose that the wild cardoon accession was *spsp/*$sp_{Leaf}sp_{Leaf}$ and "Est" was *Spsp/* $Sp_{Leaf}sp_{Leaf}$. With respect to head color, Cravero *et al.* (2005) showed that within globe artichoke, two independent genes act epistatically to determine the trait; in the absence of dominant alleles at *P* the inflorescence bracts remain green (*pp*), while the genotype *P-U-* develops purple-green bracts and *P-uu* uniformly purple bracts. The segregation for head color observed in the present mapping population was consistent with homozygosity composition in both parents at locus *P*, which determines the presence/absence of anthocyanic pigments (*pp* in "Wild" and *PP* in "Est"), while "Wild" was *Uu* and "Est" was *uu;* suggesting that the second locus, which determinates anthocyanin distribution, segregated. The *U* locus mapped on the maternal map to Wild_Va.

The alignment and integration of independently generated linkage maps is desirable, but problematical where different marker types and/or population types are involved (Sun *et al*. 2007). Here, we relied on a set of 48 co-dominant markers for the alignment with the Portis *et al*. (2012) "Romanesco C3" x "Altilis 41" consensus map. This allowed 16 of the "Wild" and 11 of the "Est" LGs to be matched with 16 out of the 17 consensus LGs. Six of the reference LGs could be simultaneously aligned with both the "Wild" and "Est" LGs, leaving seven aligned only with the "Wild" map and four with only the "Est" map. The number of bridging markers per LG required for this exercise varied from one to four, and their linear order was mostly conserved. The exceptions related to three of the CELMS and four of the CyEM SSRs, which appeared to identify small inversions within LGs III, VIII and XV. Such minor differences may be due to mapping imprecisions (Lombard and Delourme 2001), to differences in recombination frequencies of marker pairs in different populations (Studer et al. 2010) or might be attributed to different population sizes (Spiller et al. 2011). Other potential sources of variation are genotyping errors, an excess of missing values and the mapping of distorted markers (Hackett and Broadfoot 2003). Given the probabilistic nature of genetic maps, the re-ordering of tightly linked

markers will generally produce a version of the map only marginally less probable than the most probable one, so this practice is quite frequently followed to improve alignment quality (Cervera *et al*. 2001; Jeuken *et al*. 2001; Lespinasse *et al*. 2000; Lombard and Delourme 2001; Sebastian *et al*. 2000). The further alignment of the "Wild" and "Est" LGs with 15 of the Sonnante *et al*. (2011) globe artichoke x wild cardoon LGs using 31 common markers evidenced the assignment of 14 SSR loci (ten CyEM, four CELMS) to a specific LG for the first time in a *C. cardunculus* map.

Given that the parents of the present mapping population differ widely with respect to a number of both qualitative and quantitative traits such as shape and weight of the heads; number of head per plant; height and shape of the plant; days to first harvest, opportunities are now available to investigate the inheritance of some important agronomic characteristics. Moreover, these are the first linkage maps of *C. cardunculus* developed from Argentinean genotypes of wild cardoon and globe artichoke. The enrichment of these maps with additional markers, like CAPS and SNPs recently developed by Scaglione *et al*. (2012a, 2012b), will improve their utility for the localization of major genes and quantitative trait loci.

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Tables

Table 1 SRAP primer sequences used for genotyping.

Forward Primer		**Reverse Primer**	
Me1	5’-TGAGTCCAAACCGGATA-3’	**Em1**	5’-GACTGCGTACGAATTAAT-3’
Me2	5’-TGAGTCCAAACCGGAGC-3’	**Em2**	5’-GACTGCGTACGAATTTGC-3’
Me3	5’-TGAGTCCAAACCGGAAT-3’	**Em3**	5’-GACTGCGTACGAATTGAC-3’
Me4	5’-TGAGTCCAAACCGGACC-3’	**Em4**	5’-GACTGCGTACGAATTTGA-3’
Me5	5’-TGAGTCCAAACCGGAAG-3’	**Em5**	5’-GACTGCGTACGAATTAAC-3’

Table 2 AFLP primer combinations used for genotyping.

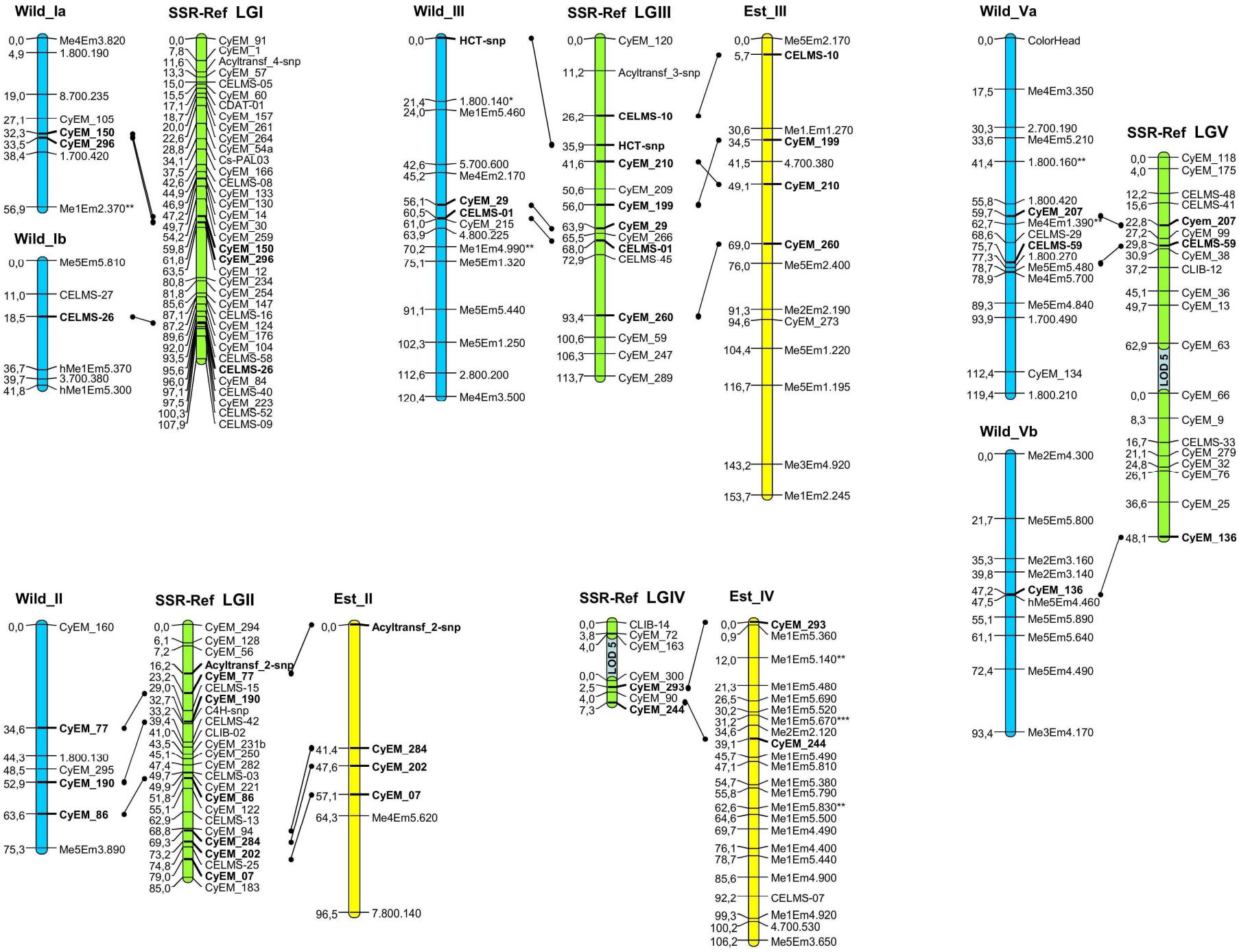
EcoRI/TaqI template	
Primer combination	**Code**
E + ACC/T + TTT	1.800
E + ACG/T + TTT	1.700
E + ACC/T + TAC	2.800
E + ACG/T + TAC	2.700
E + ACC/T + TGT	3.800
E + ACG/T + TGT	3.700
E + ACC/T + TAG	4.800
E + ACG/T + TAG	4.700
E + ACC/T + TAT	5.800
E + ACG/T + TAT	5.700
E + ACC/T + TCC	6.800
E + ACG/T + TCC	6.700
E + ACC/T + TAA	7.800
E + ACG/T + TAA	7.700
E + ACC/T + TTA	8.800
E + ACG/T + TTA	8.700

Table 3 Key characteristics of the wild cardoon ("Wild") and globe artichoke ("Est") linkage maps and their alignment.

LG name		Size (cM) Wild	Size (cM) Est	Total markers	Marker density	Portis *et al.* 2012		Sonnante *et al.* 2011	
Wild cardoon	**Estrella del Sur**					**Aligned LGs**	**Shared markers**	**Aligned LGs**	**Shared markers**
Wild_Ia		56,9		8	8,1	I	2	I	2
Wild_Ib		41,8		6	8,4		1		0
Wild_II		75,3		7	12,6	II	3	II	2
	Est_II		96,5	6	19,3		4		1
Wild_III		120,4		15	8,6	III	3	III	1
	Est_III		153,7	14	11,8		4		0
	Est_IV		106,2	23	4,8	IV	2	VI	2
Wild_Va		119,4		17	7,5	V	2	V	2
Wild_Vb		93,4		10	10,4		1	X	1
Wild_VI		119,1		10	13,2	VI	2		0
Wild_VII		105,7		16	7,0	VII	2	XVIII	2
Wild_VIII		153,1		34	4,6	VIII	2	XV	1
	Est_VIIIa		120,3	23	5,5		3	VIII	1
	Est_VIIIb		18,5	4	6,2		1	VIII	2
Wild_IX		59,9		5	15,0	IX	2	IX	2
	Est_IX		31,4	4	10,5		2		2
	Est_Xa		12,4	3	6,2	X	3	XI	1
	Est_Xb		70,6	20	3,7		1		1
Wild_XI		108,4		10	12,0	XI	2		0
	Est_XI		36,1	9	4,5		0		0
Wild_XII		67,4		23	3,1	XII	1	IV	1
	Est_XII		92,8	18	5,5		0		1
Wild_XIII		125,8		16	8,4	XIII	1	XIV	1
Wild_XIV		136,4		26	5,5	XIV	1	XIII	1
Wild_XVa		52,4		6	10,5	XV	1	XVI	1
Wild_XVb		30,1		5	7,5		3		3
	Est_XVII		121,1	12	11,0	XVII	1		0
	Est_n.a.		50,5	5	12,6		0		0

Figure caption

Figure 1 (A, B, C) Genetic linkage maps of wild cardoon (blue LGs, shown on the left) and globe artichoke (yellow LGs, on the right) aligned with the reference SSR-based consensus map (green LGs in the center). Shared SSR and SNP loci are shown in bold, and their positions are connected by a line. Marker names are shown to the right of each LG, with map distances (in cM) to the left. Markers showing significant levels of segregation distortion are indicated by asterisks (*: 0.1 >P < 0.05, **: 0.05 >P < 0.01, *** P > 0.01).


Wild_Ia
0,0 Me4Em3.820
4,9 1.800.190
19,0 8.700.235
27,1 CyEM_105
32,3 CyEM_150
33,5 CyEM_296
38,4 1.700.420
56,9 Me1Em2.370**
Wild_Ib
0,0 Me5Em5.810
11,0 CELMS-27
18,5 CELMS-26
36,7 hMe1Em5.370
39,7 3.700.380
41,8 hMe1Em5.300
SSR-Ref LGI
0,0 CyEM_91
7,8 CyEM_1
11,6 Acyltransf_4-snp
13,3 CyEM_57
15,0 CELMS-05
15,5 CyEM_60
17,1 CDAT-01
18,7 CyEM_157
20,0 CyEM_261
22,6 CyEM_264
28,8 CyEM_54a
34,1 Cs-PAL03
37,5 CyEM_166
42,6 CELMS-08
44,9 CyEM_133
46,9 CyEM_130
47,2 CyEM_14
49,7 CyEM_30
54,2 CyEM_259
59,8 CyEM_150
61,8 CyEM_296
63,5 CyEM_12
80,8 CyEM_234
81,8 CyEM_254
85,6 CyEM_147
87,1 CELMS-16
87,2 CyEM_124
89,6 CyEM_176
92,0 CyEM_104
93,5 CELMS-58
95,6 CELMS-26
96,0 CyEM_84
97,1 CELMS-40
97,5 CyEM_223
100,3 CELMS-52
107,9 CELMS-09
Wild_III
0,0 HCT-snp
21,4 1.800.140*
24,0 Me1Em5.460
42,6 5.700.600
45,2 Me4Em2.170
56,1 CyEM_29
60,5 CELMS-01
61,0 CyEM_215
63,9 4.800.225
70,2 Me1Em4.990**
75,1 Me5Em1.320
91,1 Me5Em5.440
102,3 Me5Em1.250
112,6 2.800.200
120,4 Me4Em3.500
SSR-Ref LGIII
0,0 CyEM_120
11,2 Acyltransf_3-snp
26,2 CELMS-10
35,9 HCT-snp
41,6 CyEM_210
50,6 CyEM_209
56,0 CyEM_199
63,9 CyEM_29
65,5 CyEM_266
68,0 CELMS-01
72,9 CELMS-45
93,4 CyEM_260
100,6 CyEM_59
106,3 CyEM_247
113,7 CyEM_289
Est_III
0,0 Me5Em2.170
5,7 CELMS-10
30,6 Me1.Em1.270
34,5 CyEM_199
41,5 4.700.380
49,1 CyEM_210
69,0 CyEM_260
76,0 Me5Em2.400
91,3 Me2Em2.190
94,6 CyEM_273
104,4 Me5Em1.220
116,7 Me5Em1.195
143,2 Me3Em4.920
153,7 Me1Em2.245
Wild_Va
0,0 ColorHead
17,5 Me4Em3.350
30,3 2.700.190
33,6 Me4Em5.210
41,4 1.800.160**
55,8 1.800.420
59,7 CyEM_207
62,7 Me4Em1.390**
68,6 CELMS-29
75,7 CELMS-59
77,3 1.800.270
78,7 Me5Em5.480
78,9 Me4Em5.700
89,3 Me5Em4.840
93,9 1.700.490
112,4 CyEM_134
119,4 1.800.210
SSR-Ref LGV
0,0 CyEM_118
4,0 CyEM_175
12,2 CELMS-48
15,6 CELMS-41
22,8 Cyem_207
27,2 CyEM_99
29,8 CELMS-59
30,9 CyEM_38
37,2 CLIB-12
45,1 CyEM_36
49,7 CyEM_13
62,9 CyEM_63
LOD 5
0,0 CyEM_66
8,3 CyEM_9
16,7 CELMS-33
21,1 CyEM_279
24,8 CyEM_32
26,1 CyEM_76
36,6 CyEM_25
48,1 CyEM_136
Wild_Vb
0,0 Me2Em4.300
21,7 Me5Em5.800
35,3 Me2Em3.160
39,8 Me2Em3.140
47,2 CyEM_136
47,5 hMe5Em4.460
55,1 Me5Em5.890
61,1 Me5Em5.640
72,4 Me5Em4.490
93,4 Me3Em4.170
Wild_II
0,0 CyEM_160
34,6 CyEM_77
44,3 1.800.130
48,5 CyEM_295
52,9 CyEM_190
63,6 CyEM_86
75,3 Me5Em3.890
SSR-Ref LGII
0,0 CyEM_294
6,1 CyEM_128
7,2 CyEM_56
16,2 Acyltransf_2-snp
23,2 CyEM_77
29,0 CELMS-15
32,7 CyEM_190
33,2 C4H-snp
39,4 CELMS-42
41,0 CLIB-02
43,5 CyEM_231b
45,1 CyEM_250
47,4 CyEM_282
49,7 CELMS-03
49,9 CyEM_221
51,8 CyEM_86
55,1 CyEM_122
62,9 CELMS-13
68,8 CyEM_94
69,3 CyEM_284
73,2 CyEM_202
74,8 CELMS-25
79,0 CyEM_07
85,0 CyEM_183
Est_II
0,0 Acyltransf_2-snp
41,4 CyEM_284
47,6 CyEM_202
57,1 CyEM_07
64,3 Me4Em5.620
96,5 7.800.140
SSR-Ref LGIV
0,0 CLIB-14
3,8 CyEM_72
4,0 CyEM_163
LOD 5
0,0 CyEM_300
2,5 CyEM_293
4,0 CyEM_90
7,3 CyEM_244
Est_IV
0,0 CyEM_293
0,9 Me1Em5.360
12,0 Me1Em5.140**
21,3 Me1Em5.480
26,5 Me1Em5.690
30,2 Me1Em5.520
31,2 Me1Em5.670***
34,6 Me2Em2.120
39,1 CyEM_244
45,7 Me1Em5.490
47,1 Me1Em5.810
54,7 Me1Em5.380
55,8 Me1Em5.790
62,6 Me1Em5.830**
64,6 Me1Em5.500
69,7 Me1Em4.490
76,1 Me1Em4.400
78,7 Me1Em5.440
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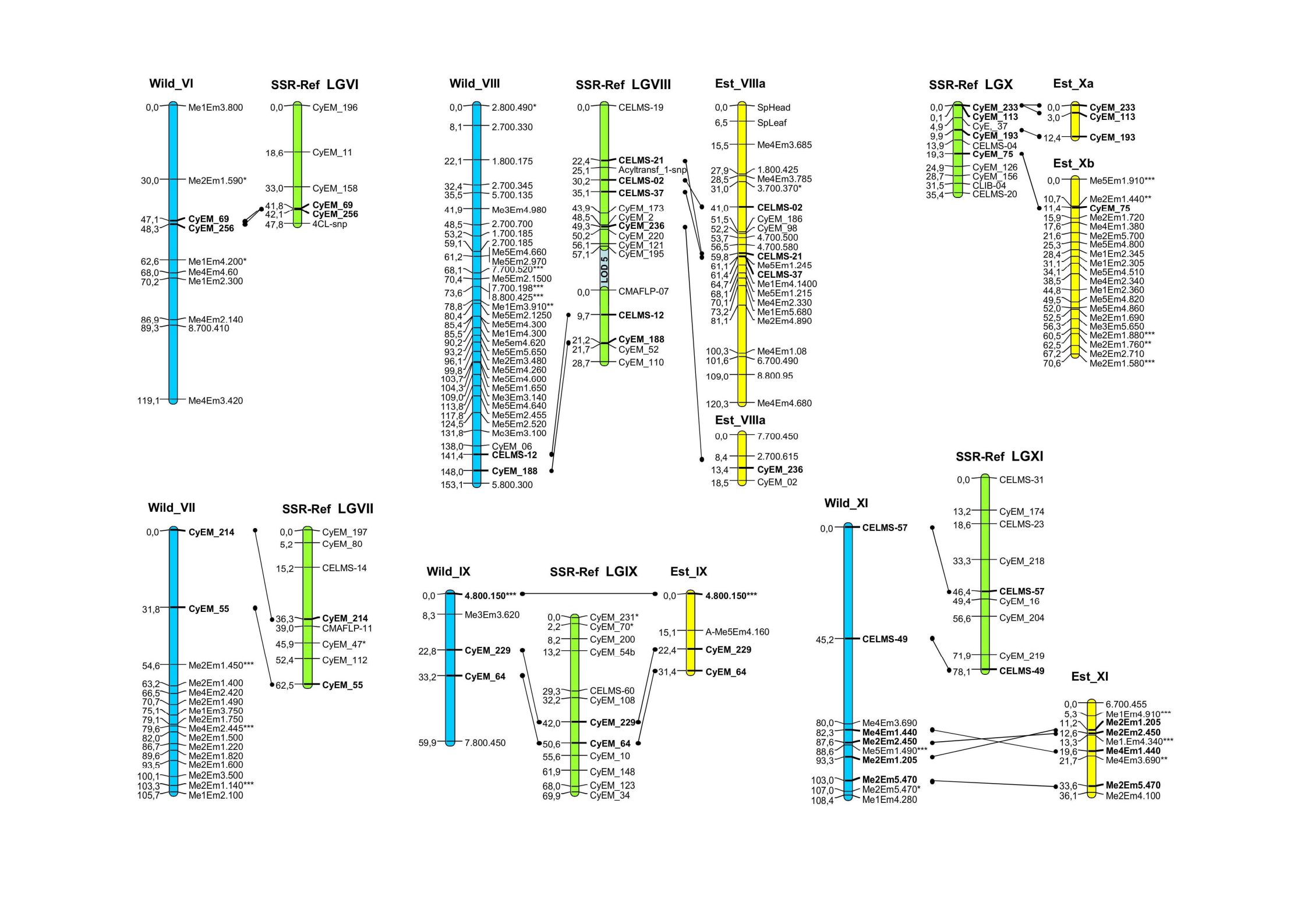
99,3 Me1Em4.920
100,2 4.700.530
106,2 Me5Em3.650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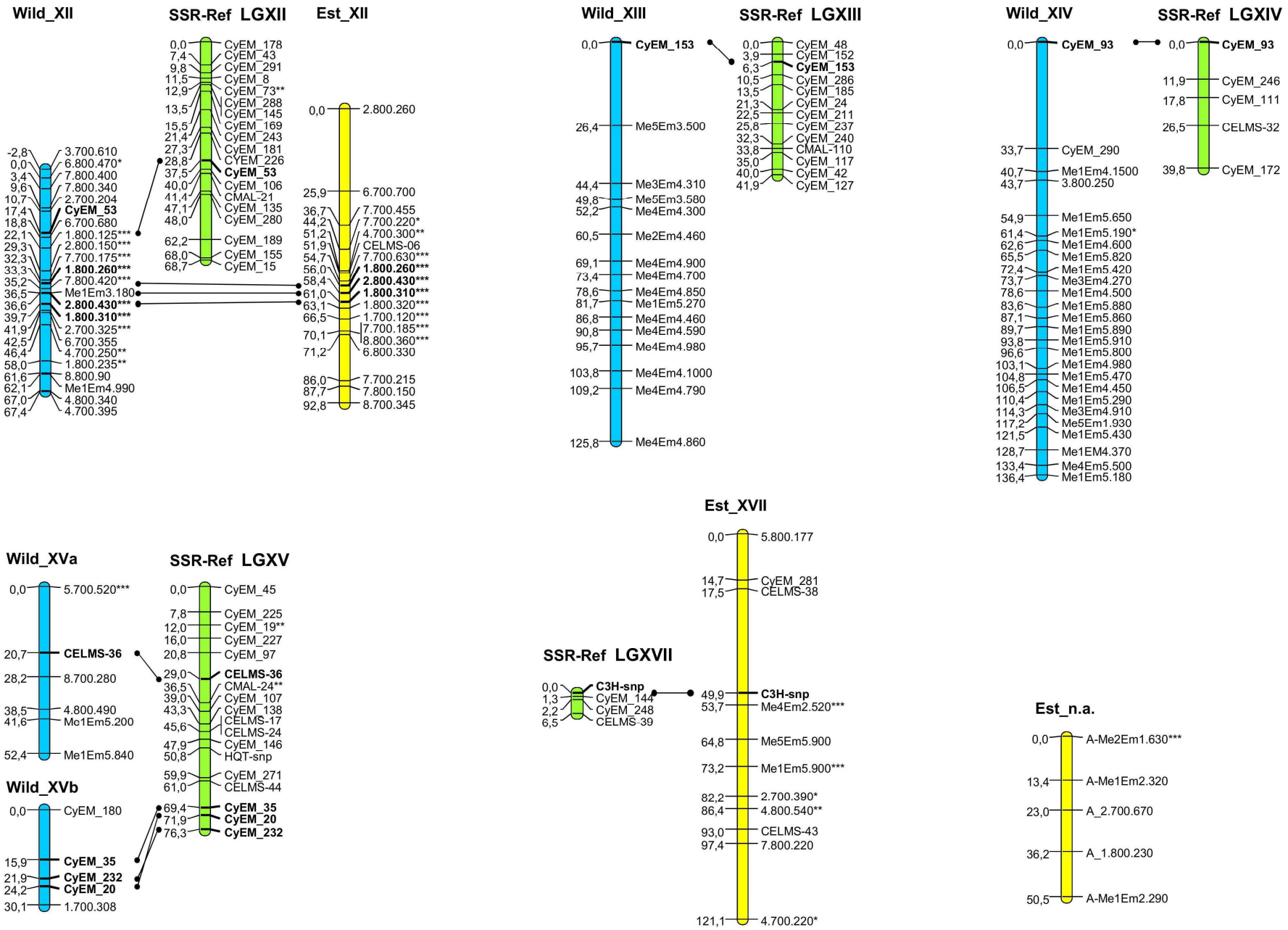
30,0 Me2Em1.590*
47,1 CyEM_69
48,3 CyEM_256
62,6 Me1Em4.200*
68,0 Me4Em4.60
70,2 Me1Em2.300
86,9 Me4Em2.140
89,3 8.700.410
119,1 Me4Em3.420
SSR-Ref LGVI
0,0 CyEM_196
18,6 CyEM_11
33,0 CyEM_158
41,8 CyEM_69
42,1 CyEM_256
47,8 4CL-snp
Wild_VIII
0,0 2.800.490*
8,1 2.700.330
22,1 1.800.175
32,4 2.700.345
35,5 5.700.135
41,9 Me3Em4.980
48,5 2.700.700
53,2 1.700.185
59,1 2.700.185
61,2 Me5Em4.660
Me5Em2.970
68,1 7.700.520***
70,4 Me5Em2.1500
73,6 7.700.198***
8.800.425***
78,8 Me1Em3.910**
80,4 Me5Em2.1250
85,4 Me5Em4.300
85,5 Me1Em4.300
90,2 Me5em4.620
93,2 Me5Em5.650
96,1 Me2Em3.480
99,8 Me5Em4.260
103,7 Me5Em4.600
104,3 Me5Em1.650
109,0 Me3Em3.140
113,8 Me5Em4.640
117,8 Me5Em2.455
124,5 Me5Em2.520
131,8 Me3Em3.100
138,0 CyEM_06
141,4 CELMS-12
148,0 CyEM_188
153,1 5.800.300
SSR-Ref LGVIII
0,0 CELMS-19
22,4 CELMS-21
25,1 Acyltransf_1-snp
30,2 CELMS-02
35,1 CELMS-37
43,9 CyEM_173
48,5 CyEM_2
49,3 CyEM_236
50,2 CyEM_220
56,1 CyEM_121
57,1 CyEM_195
LOD 5
0,0 CMAFLP-07
9,7 CELMS-12
21,2 CyEM_188
21,7 CyEM_52
28,7 CyEM_110
Est_VIIIa
0,0 SpHead
6,5 SpLeaf
15,5 Me4Em3.685
27,9 1.800.425
28,5 Me4Em3.785
31,0 3.700.370*
41,0 CELMS-02
51,5 CyEM_186
52,2 CyEM_98
53,7 4.700.500
56,5 4.700.580
59,8 CELMS-21
61,1 Me5Em1.245
61,4 CELMS-37
64,7 Me1Em4.1400
68,1 Me5Em1.215
70,1 Me4Em2.330
73,2 Me1Em5.680
81,1 Me2Em4.890
100,3 Me4Em1.08
101,6 6.700.490
109,0 8.800.95
120,3 Me4Em4.680
Est_VIIIa
0,0 7.700.450
8,4 2.700.615
13,4 CyEM_236
18,5 CyEM_02
SSR-Ref LGX
0,0 CyEM_233
0,1 CyEM_113
4,9 CyE_37
9,9 CyEM_193
13,9 CELMS-04
19,3 CyEM_75
24,9 CyEM_126
28,7 CyEM_156
31,5 CLIB-04
35,4 CELMS-20
Est_Xa
0,0 CyEM_233
3,0 CyEM_113
12,4 CyEM_193
Est_Xb
0,0 Me5Em1.910***
10,7 Me2Em1.440**
11,4 CyEM_75
15,9 Me2Em1.720
17,6 Me4Em1.380
21,6 Me2Em5.700
25,3 Me5Em4.800
28,4 Me1Em2.345
31,1 Me1Em2.305
34,1 Me5Em4.510
38,5 Me4Em2.340
44,8 Me1Em2.360
49,5 Me5Em4.820
52,0 Me5Em4.860
52,5 Me2Em1.690
56,3 Me3Em5.650
60,5 Me2Em1.880***
62,5 Me2Em1.760**
67,2 Me2Em2.710
70,6 Me2Em1.580***
Wild_VII
0,0 CyEM_214
31,8 CyEM_55
54,6 Me2Em1.450***
63,2 Me2Em1.400
66,5 Me4Em2.420
70,7 Me2Em1.490
75,1 Me1Em3.750
79,1 Me2Em1.750
79,6 Me4Em2.445***
82,0 Me2Em1.500
86,7 Me2Em1.220
89,6 Me2Em1.820
93,5 Me2Em1.600
100,1 Me2Em3.500
103,3 Me2Em1.140***
105,7 Me1Em2.100
SSR-Ref LGVII
0,0 CyEM_197
5,2 CyEM_80
15,2 CELMS-14
36,3 CyEM_214
39,0 CMAFLP-11
45,9 CyEM_47*
52,4 CyEM_112
62,5 CyEM_55
Wild_IX
0,0 4.800.150***
8,3 Me3Em3.620
22,8 CyEM_229
33,2 CyEM_64
59,9 7.800.450
SSR-Ref LGIX
0,0 CyEM_231*
2,2 CyEM_70*
8,2 CyEM_200
13,2 CyEM_54b
29,3 CELMS-60
32,2 CyEM_108
42,0 CyEM_229
50,6 CyEM_64
55,6 CyEM_10
61,9 CyEM_148
68,0 CyEM_123
69,9 CyEM_34
Est_IX
0,0 4.800.150***
15,1 A-Me5Em4.160
22,4 CyEM_229
31,4 CyEM_64
Wild_XI
0,0 CELMS-57
45,2 CELMS-49
80,0 Me4Em3.690
82,3 Me4Em1.440
87,6 Me2Em2.450
88,6 Me5Em1.490***
93,3 Me2Em1.205
103,0 Me2Em5.470
107,0 Me2Em5.470*
108,4 Me1Em4.280
SSR-Ref LGXI
0,0 CELMS-31
13,2 CyEM_174
18,6 CELMS-23
33,3 CyEM_218
46,4 CELMS-57
49,4 CyEM_16
56,6 CyEM_204
71,9 CyEM_219
78,1 CELMS-49
Est_XI
0,0 6.700.455
5,3 Me1Em4.910***
11,2 Me2Em1.205
12,6 Me2Em2.450
13,3 Me1.Em4.340***
19,6 Me4Em1.440
21,7 Me4Em3.690**
33,6 Me2Em5.470
36,1 Me2Em4.100


Wild_XII
SSR-Ref LGXII
Est_XII
-2,8 3.700.610
0,0 6.800.470*
3,4 7.800.400
9,6 7.800.340
10,7 2.700.204
17,4 CyEM_53
18,8 6.700.680
22,1 1.800.125***
29,3 2.800.150***
32,3 7.700.175***
33,3 1.800.260***
35,2 7.800.420***
36,5 Me1Em3.180
36,6 2.800.430***
39,7 1.800.310***
41,9 2.700.325***
42,5 6.700.355
46,4 4.700.250**
58,0 1.800.235**
61,6 8.800.90
62,1 Me1Em4.990
67,0 4.800.340
67,4 4.700.395
0,0 CyEM_178
7,4 CyEM_43
9,8 CyEM_291
11,5 CyEM_8
12,9 CyEM_73**
13,5 CyEM_288
CyEM_145
15,5 CyEM_169
21,4 CyEM_243
27,3 CyEM_181
28,8 CyEM_226
37,5 CyEM_53
40,0 CyEM_106
41,4 CMAL-21
47,1 CyEM_135
48,0 CyEM_280
62,2 CyEM_189
68,0 CyEM_155
68,7 CyEM_15
0,0 2.800.260
25,9 6.700.700
36,7 7.700.455
44,2 7.700.220*
51,2 4.700.300**
51,9 CELMS-06
54,7 7.700.630***
56,0 1.800.260***
58,4 2.800.430***
61,0 1.800.310***
63,1 1.800.320***
66,5 1.700.120***
70,1 7.700.185***
8.800.360***
71,2 6.800.330
86,0 7.700.215
87,7 7.800.150
92,8 8.700.345
Wild_XIII
SSR-Ref LGXIII
0,0 CyEM_153
26,4 Me5Em3.500
44,4 Me3Em4.310
49,8 Me5Em3.580
52,2 Me4Em4.300
60,5 Me2Em4.460
69,1 Me4Em4.900
73,4 Me4Em4.700
78,6 Me4Em4.850
81,7 Me1Em5.270
86,8 Me4Em4.460
90,8 Me4Em4.590
95,7 Me4Em4.980
103,8 Me4Em4.1000
109,2 Me4Em4.790
125,8 Me4Em4.860
0,0 CyEM_48
3,9 CyEM_152
6,3 CyEM_153
10,5 CyEM_286
13,5 CyEM_185
21,3 CyEM_24
22,5 CyEM_211
25,8 CyEM_237
32,3 CyEM_240
33,8 CMAL-110
35,0 CyEM_117
40,0 CyEM_42
41,9 CyEM_127
Wild_XIV
SSR-Ref LGXIV
0,0 CyEM_93
33,7 CyEM_290
40,7 Me1Em4.1500
43,7 3.800.250
54,9 Me1Em5.650
61,4 Me1Em5.190*
62,6 Me1Em4.600
65,5 Me1Em5.820
72,4 Me1Em5.420
73,7 Me3Em4.270
78,6 Me1Em4.500
83,6 Me1Em5.880
87,1 Me1Em5.860
89,7 Me1Em5.890
93,8 Me1Em5.910
96,6 Me1Em5.800
103,1 Me1Em4.980
104,8 Me1Em5.470
106,5 Me1Em4.450
110,4 Me1Em5.290
114,3 Me3Em4.910
117,2 Me5Em1.930
121,5 Me1Em5.430
128,7 Me1EM4.370
133,4 Me4Em5.500
136,4 Me1Em5.180
0,0 CyEM_93
11,9 CyEM_246
17,8 CyEM_111
26,5 CELMS-32
39,8 CyEM_172
Wild_XVa
SSR-Ref LGXV
0,0 5.700.520***
20,7 CELMS-36
28,2 8.700.280
38,5 4.800.490
41,6 Me1Em5.200
52,4 Me1Em5.840
0,0 CyEM_45
7,8 CyEM_225
12,0 CyEM_19**
16,0 CyEM_227
20,8 CyEM_97
29,0 CELMS-36
36,5 CMAL-24**
39,0 CyEM_107
43,3 CyEM_138
45,6 CELMS-17
CELMS-24
47,9 CyEM_146
50,8 HQT-snp
59,9 CyEM_271
61,0 CELMS-44
Wild_XVb
0,0 CyEM_180
15,9 CyEM_35
21,9 CyEM_232
24,2 CyEM_20
30,1 1.700.308
69,4 CyEM_35
71,9 CyEM_20
76,3 CyEM_232
Est_XVII
SSR-Ref LGXVII
0,0 C3H-snp
1,3 CyEM_144
2,2 CyEM_248
6,5 CELMS-39
0,0 5.800.177
14,7 CyEM_281
17,5 CELMS-38
49,9 C3H-snp
53,7 Me4Em2.520***
64,8 Me5Em5.900
73,2 Me1Em5.900***
82,2 2.700.390*
86,4 4.800.540**
93,0 CELMS-43
97,4 7.800.220
121,1 4.700.220*
Est_n.a.
0,0 A-Me2Em1.630***
13,4 A-Me1Em2.320
23,0 A_2.700.670
36,2 A_1.800.230
50,5 A-Me1Em2.290